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Invaders eating invaders: potential trophic interactions between the amphipod *Dikerogammarus villosus* and juvenile crayfish *Orconectes limosus*

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ABSTRACT

Key-words: *invasive species, interactions, intra-guild predation, survival, crayfish*

We investigated potential interspecific predation between two invasive crustacean species, currently widespread and co-occurring in European inland waters: the Ponto-Caspian amphipod *Dikerogammarus villosus* (Gammaridae) and the North American spiny-cheek crayfish *Orconectes limosus* (Cambaridae). We evaluated interactions of adult specimens of *D. villosus* and juvenile *O. limosus* (from the 3rd developmental stage – DS) under conditions with and without feeding. We used two different experimental setups: short-term (one-week) rearing in aquaria each containing 30 specimens of either single-species or mixed stock, and 20-day-long rearing in small circular plates with one individual of each species. In the aquaria, a significant effect of *D. villosus* presence on survival of *O. limosus* stocks was found, with stronger influence on unfed stocks. Survival of *D. villosus* was not influenced by either *O. limosus* presence or feeding. Direct predation of *D. villosus* on juvenile *O. limosus*, predominantly on the 3rd DS, was often observed in the small plates. The 5th DS *O. limosus* was killed only a few times and was already able to feed on adult *D. villosus*. Our results show that both species are able to affect each other negatively through intra-guild predation: *D. villosus* may successfully feed on juvenile *O. limosus* (3rd and 4th DS), but larger crayfish can resist predation by the amphipod.

RÉSUMÉ

Une espèce invasive mangeant une autre espèce invasive : interactions trophiques potentielles entre l'amphipode *Dikerogammarus villosus* et le juvénile de l'écrevisse *Orconectes limosus*

Mots-clés : *espèce invasive, interactions, prédation intra-guilde, survie, écrevisse*

Nous avons étudié la prédation potentielle interspécifique entre deux espèces de crustacé invasives, aujourd'hui très répandues et coexistant dans les eaux intérieures européennes : l'amphipode Ponto-Caspien *Dikerogammarus villosus* (Gammaridae) et l'écrevisse américaine *Orconectes limosus* (Cambaridae). Nous avons évalué les interactions entre des spécimens adultes de *D. villosus* et des juvéniles d'*O. limosus* (à partir du stade 3 de développement) en présence ou non d'autre nourriture. Nous avons utilisé deux dispositifs expérimentaux : élevage de court terme (une semaine) dans des aquariums contenant chacun 30 individus,

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soit monospécifique soit bispécifique, et un élevage de 20 jours en plateau circulaire avec un individu de chaque espèce. En aquarium, un effet significatif de la présence de *D. villosus* sur la survie d'*O. limosus* a été trouvé, avec un effet plus fort dans les lots non nourris. La survie de *D. villosus* n'a été influencée ni par la présence d'*O. limosus* ni par le nourrissage. Une prédation directe de *D. villosus* sur les juvéniles d'*O. limosus*, principalement sur le stade 3, a été souvent observée dans les expériences de 20 jours. Le stade 5 d'*O. limosus* n'a été tué que quelque fois et est capable aussi de se nourrir de *D. villosus*. Nos résultats montrent que les deux espèces sont capables d'interagir négativement par prédation : *D. villosus* peut se nourrir avec des juvéniles d'*O. limosus* (stade 3 et 4) mais les écrevisses plus grandes peuvent résister à la prédation de l'amphipode.

INTRODUCTION

Increased spread of alien species in European waters results not only in contact between native and invasive species, but also between invaders from different biogeographic regions which may directly interact with each other. Among a number of alien crustacean taxa spreading through Central European watercourses, two groups are particularly interesting for their invasiveness and ability to affect their related native counterparts – North American crayfish (Holdich and Pöckl, 2007) and Ponto-Caspian amphipods (Bij de Vaate *et al.*, 2002). One of the major European rivers where representatives of both groups come into contact is the Elbe. The American spiny-cheek crayfish *Orconectes limosus* (Rafinesque, 1817) and the amphipod *Dikerogammarus villosus* (Sowinsky, 1894) co-occur along most of its stretch, including the part in the Czech Republic (Petrusek, 2006a, 2006b). In our study, we focused on some aspects of potential interactions of these two invasive species.

The spiny-cheek crayfish was the first non-indigenous crayfish deliberately introduced into Europe from the North American continent (Holdich, 2002). It is now one of the most common crayfish in continental Europe, present in at least 20 countries (Holdich *et al*., 2006), and still spreading (*e.g.*, Pârvulescu *et al.*, 2009). The colonization speed of *O. limosus* in the River Danube was calculated to be over 13 km·yr^{-1} (Puky and Schád, 2006). *Orconectes limosus* has a short life span, usually less than four years (Hamr, 2002), acts as a vector of crayfish plague (Cerenius *et al.*, 1988; Kozubíková *et al.*, 2009) and its life cycle differs from that of European native crayfish (Stucki, 2002; Buřič *et al.*, 2009). Other characteristics improving its invasive potential is high fecundity (Kozák *et al.*, 2006), activity (Musil *et al.*, 2009) and aggressiveness (Holdich and Black, 2007), and a great tolerance to unfavorable conditions (Holdich *et al.*, 2006). Overall, *O. limosus* is a fast-spreading invasive species that poses a serious threat to indigenous crayfish species in Europe. It invaded the territory of the Czech Republic through the River Elbe in approximately the 1960s and is presently widespread in the western part of the country (Petrusek *et al.*, 2006).

Dikerogammarus villosus is an invasive Ponto-Caspian species which invaded new localities in Central and Western Europe through the southern (Bij de Vaate *et al.*, 2002) and central (Pöckl, 2009) migration corridors. Recently it has become very common and abundant in a number of European river systems (Füreder and Pöckl, 2007), where it has a significant impact on other biota by competition, and predominantly by high predatory capabilities on other aquatic macroinvertebrates, including amphipods (Dick and Platvoet, 2000; Platvoet *et al.*, 2009), an isopod (Krisp and Maier, 2005), aquatic insects (Dick *et al.*, 2002; Füreder and Pöckl, 2007) and even small fish (Casellato *et al.*, 2007). *D. villosus* is a very adaptable species (Füreder and Pöckl, 2007) with high temperature and salinity tolerance (Bruijs *et al.*, 2001). It is competitively superior to many of the indigenous amphipod species in its life history variables, including early maturation, rapid growth and high fecundity (Devin *et al.*, 2004; Füreder and Pöckl, 2007). The invasion by this species of the Elbe is a recent phenomenon: since reaching it through canals in Germany around 1998 (Bij de Vaate *et al.*, 2002), it has spread to the Czech territory within five years (Petrusek, 2006b).

Although *O. limosus* and *D. villosus* co-occur in various European river systems (Holdich and Pöckl, 2007), their potential inter-specific interactions are unknown. According to their ecological characteristics (Füreder and Pöckl, 2007), it can be expected that each of the two species has potential to feed on at least some developmental stages of the other one. The present study is the first contribution to evaluating these invader-invader interactions. Specifically, we tested the hypothesis that *D. villosus* may have substantial impact on newly independent *O. limosus* juveniles (*i.e.*, from the 3rd developmental stage), and also assessed potential effects of juvenile crayfish on the amphipods.

MATERIAL AND METHODS

> ANIMALS

Orconectes limosus juveniles were obtained from 45 females (carapace length 32.7 ± 3.06 mm, mean ± SD) reared under natural ambient photoperiod and water temperature in the experimental department of the Research Institute of Fish Culture and Hydrobiology (RIFCH) in Vodňany. Juveniles were separated from their mothers when they became independent, *i.e.*, at the 3rd developmental stage (DS) (Andrews, 1907). The experimental animals were selected randomly from a mixed stock of juveniles from all females.

Dikerogammarus villosus adult specimens were collected at the lower reaches of the Czech section of the River Elbe from shallow rocky habitats. They were transported to the experimental department of the RIFCH in Vodňany and acclimated for two weeks in conditions similar to those in subsequent experiments. Experimental animals were chosen randomly from available *D. villosus* specimens, including both males and females.

> EXPERIMENTAL SETUP

Aquaria

The rearing was carried out for one week, from June 5 to June 12, 2007. An independent recirculation system was used as a water supply with aeration in each aquarium. Six treatments (each in triplicate) were prepared: single stock of *O. limosus* 3rd DS, single stock of *D. villosus*; and mixed stock of *O. limosus* 3rd DS and *D. villosus*, each of these in both fed and unfed variants. Each single-species treatment consisted of 30 specimens; mixed treatments consisted of 15 specimens of each species. The fed treatments were provided with live zooplankton in excess daily. The number of surviving individuals was evaluated for each species in each aquarium at the end of the experiment.

To ensure the environmental conditions of aquaria were comparable, dissolved oxygen (7.6 ± 0.17 $\text{mg}\cdot\text{L}^{-1}$, mean ± SD) and temperature (21.9 ± 0.63 °C) were measured twice a day using the Oxi 315i oximeter (WTW GmbH, Weilheim, Germany) and pH (7.2 ± 0.14) was measured weekly by a pH meter (315i, WTW GmbH, Weilheim, Germany); none of these parameters differed among treatments to influence the results substantially.

Circular plates

The experiment lasted from June 5 to June 26, 2007. Twenty glass plates (diameter 120 mm, depth 30 mm) were used for experimental purposes. The stock of each plate initially consisted of one *O. limosus* in the 3rd DS and one *D. villosus* specimen. The animals in ten plates were fed live zooplankton in excess daily; the remaining ones were unfed. The direct predation, mortality and molt events were recorded three times a day; only those animals which were unambiguously preyed upon were included in results. The stock of each plate where one or both specimens died was substituted with new animals from source aquaria.

Table I
Survival of individuals in particular experimental treatments. Results are presented in percentages, as mean ± SD. Different superscripts in the same column show the significant differences ($P < 0.05$).

Tableau I
Survies individuelles dans différentes expériences. Les résultats sont exprimés en moyennes de pourcentages ± SD. Les différentes lettres dans une même colonne montrent les différences significatives ($P < 0{,}05$).

Species	Treatment	Fed	Survival
O. limosus	single species	Yes	77.8 ± 6.0^a
	single species	No	43.3 ± 6.7^b
	mixed species	Yes	51.3 ± 19.2^b
	mixed species	No	20.0 ± 10.2^c
D. villosus	single species	Yes	73.3 ± 6.7^a
	single species	No	81.1 ± 1.9^a
	mixed species	Yes	77.8 ± 7.7^a
	mixed species	No	80.0 ± 6.7^a

The water in plates was changed once a week. Dissolved oxygen (7.4 ± 0.19 mg·L^{-1}) and temperature (21.6 ± 0.48 °C) were measured twice a day, and pH (6.9 ± 0.11) weekly using the same instruments as above.

> *DATA ANALYSIS*

The data were analyzed with Statistica 8.0 (StatSoft, Tulsa, USA). All values were examined for homoscedasticity by the Levene test. Three-way ANOVA with the Tukey *post hoc* test was used for comparison of survival between particular experimental treatments in the aquarium experiment. Differences in predation susceptibility of different developmental stages of *O. limosus* were evaluated using χ^2 tests with Yates' correction. The null hypothesis was rejected at $\alpha = 0.05$. Results are presented as mean ± SD.

RESULTS

> *AQUARIA*

The survival of experimental stocks in particular treatments is shown in Table I. Survival of *D. villosus* was not affected by either *O. limosus* presence or feeding, in contrast to *O. limosus* survival, that decreased due to predation by *D. villosus* as well as the lack of feeding and subsequent cannibalism (Fig. 1). We observed significantly lower survival of *O. limosus* in the unfed single-species treatment and fed mixed treatment in comparison with all *D. villosus* stocks and the *O. limosus* fed single-species treatment, and even lower survival of *O. limosus* in the unfed mixed treatment ($F = 18.09$, $P < 10^{-3}$).

> *CIRCULAR PLATES*

We observed direct predation of both *D. villosus* on *O. limosus* and *O. limosus* on *D. villosus* (Fig. 2). The predation of *D. villosus* on *O. limosus* was significantly higher in unfed stock ($\chi^2 = 10.00$; $P = 0.002$). *D. villosus* was most successful in predation on the 3rd developmental stage of *O. limosus*, which was preyed upon much more frequently than older and bigger specimens (4th and 5th DS) in both unfed ($\chi^2 = 26.60$; $P < 10^{-5}$) and fed treatments ($\chi^2 = 14.60$; $P < 10^{-3}$). *Dikerogammarus villosus* killed and consumed both recently molted and intermolt victims. The consumption of a whole juvenile crayfish every second day was

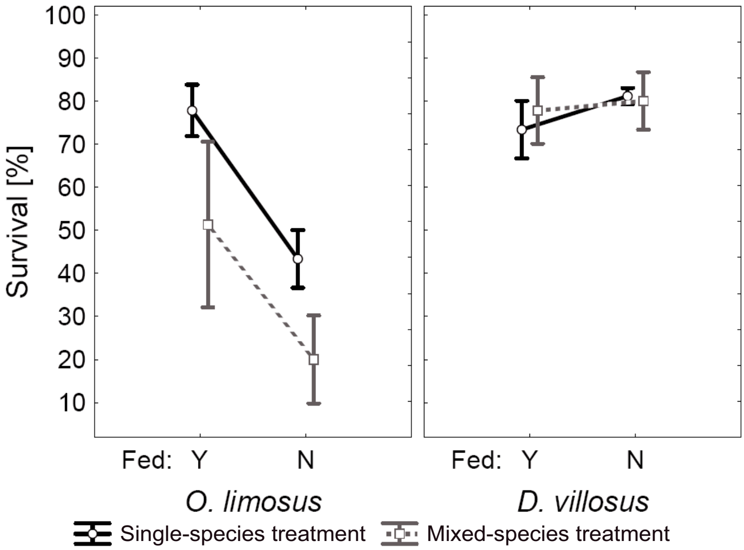

Figure 1
Significant effect of the presence of D. villosus *on* O. limosus *stocks, with stronger influence in unfed stocks (*$F = 47.87$*,* $P < 10^{-5}$*).* Dikerogammarus villosus *survival was not influenced by either* O. limosus *presence or feeding (*$F = 0.33$*,* $P = 0.576$*). Results are presented as mean ± SD.*

Figure 1
Effets significatifs de la présence de *D. villosus* sur *O. limosus*, avec une influence plus forte dans les lots sans nourriture ($F = 47{,}87$; $P < 10^{-5}$). La survie de *Dikerogammarus villosus* n'a été influencée ni par la présence d'*O. limosus* ni par le nourrissage ($F = 0{,}33$; $P = 0{,}576$). Les résultats sont des moyennes ± SD.

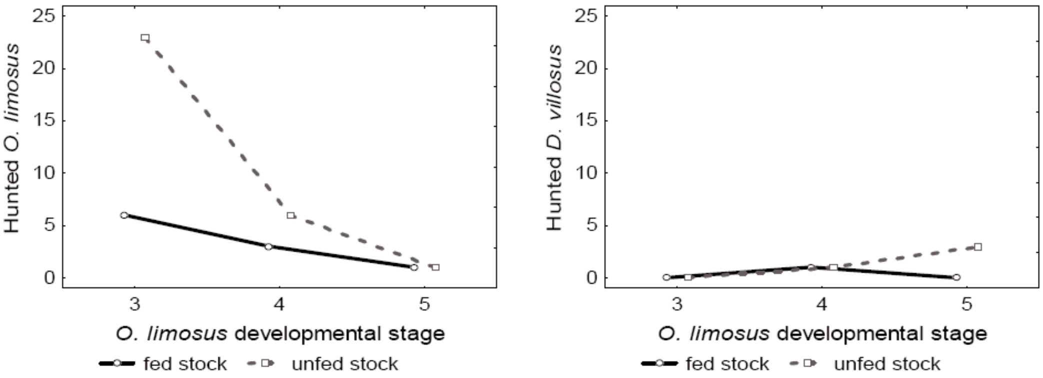

Figure 2
Number of hunted and killed (direct predation) specimens of O. limosus *by* D. villosus *(on the left) and* D. villosus *by* O. limosus *depending on the* O. limosus *developmental stage in fed and unfed treatments.*

Figure 2
Nombre d'*O. limosus* chassées et tuées (prédation directe) par *D. villosus* (sur la gauche) et *D. villosus par O. limosus* en fonction du stade de développement dans des lots nourris ou non.

observed in some *D. villosus* specimens. The 3rd DS of *O. limosus* was not able to prey on adult *D. villosus*. However, a few specimens of *D. villosus* were preyed upon by *O. limosus* 4th and 5th DS.

DISCUSSION

As presumed, both studied species were able to feed on each other. *Dikerogammarus villosus* can catch, kill and subsequently consume the juveniles of *O. limosus* from the 3rd to the 5th developmental stages, both recently molted and between molts. *D. villosus*'s ability to shred prey with a tough cuticle was reported for various prey taxa, such as other gammarid species, including their intermolts (Dick and Platvoet, 2000; Dick *et al.*, 2002), the hard-shelled water boatman *Sigara* sp. (Füreder and Pöckl, 2007), the isopod *Asellus aquaticus* (Krisp and Maier, 2005) and the mysid shrimp *Neomysis integer* (Dick *et al.*, 2002). The consumption of almost the whole juvenile crayfish every other day is in accordance with Krisp and Maier's (2005) prediction of biomass consumed daily by *D. villosus*, that can reach one-third of its own biomass.

A single case of *O. limosus* predation on *D. villosus* was observed in the 4th DS: more successful attempts were noted for the 5th DS. Therefore, we can conclude that *O. limosus* specimens were not able to effectively prey on their gammarid antagonist until the 5th DS. This is probably caused by the small size of newly independent *O. limosus* juveniles (Andrews, 1907), which may also explain the high vulnerability of *O. limosus* 3rd DS to the predation pressure of *D. villosus*, and their very low survival in both fed and unfed mixed treatments. The effect of the smaller size of *O. limosus* was also observed in interactions with *Astacus astacus* juveniles (Kozák *et al.*, 2007). The high level of cannibalism, common in juvenile *O. limosus* (Kozák *et al.*, 2007), probably reduced survival in unfed single-species stock of *O. limosus*; we did not observe a similar survival decrease in the unfed stock of the amphipod.

Our results are in accordance with the known great predatory capability of *D. villosus*. This species can fast replace native and other invasive gammarids (Dick and Platvoet, 2000; Kinzler and Maier, 2003) and cause considerable declines in the whole macroinvertebrate fauna in many communities (Devin *et al.*, 2001; Dick *et al.*, 2002). We can add early juvenile stages of crayfish to the vulnerable prey list: these are especially threatened as they occur within the macroinvertebrate community on coarse gravel and stones, known to be particularly influenced by the predaceous omnivory of *D. villosus* (van Riel *et al.*, 2006). The case of potential invader-invader interactions is interesting and could result in major or minor limitations of one or the other species; a future study may test whether adult invasive crayfish may efficiently use the amphipod as a food source. However, juveniles of native crayfish could also be influenced if *D. villosus* reaches some tributaries of large rivers where their populations occur.

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